Phytotaxa 321 (3): 287–293
http://www.mapress.com/j/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.321.3.6

Aulostemon (Asparagaceae, Scilloideae), a new genus from South Africa

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Abstract

As part of a taxonomic revision of Hyacinthaceae subfamily Urgineoideae (Asparagaceae tribe Urgineeae) based on morphological and genetic data covering numerous samples from its whole range of distribution, we here describe a new genus from south-eastern South Africa. *Aulostemon* includes *Drimia mzimvubuensis*, a species recently placed in *Sagittanthera*. However, distinct morphological character states, especially regarding connation of stamen filaments to form a distinct tube that surrounds the gynoecium, the free anthers, the lack of bracteoles and its isolated phylogenetic position within subfamily Urgineoideae, support the description of the new genus.

Key words: Hyacinthaceae, distribution, ecology, Urgineoideae, taxonomy

Introduction

Hyacinthaceae includes between 700–1000 species of bulbous plants mostly occurring in Africa, Europe and Asia, with a single genus, *Oziroë* Rafinesque (1837: 53), present in South America (Speta 1998a, b, APG 2003). Four monophyletic subfamilies are accepted in Hyacinthaceae: Hyacinthoideae, Ornithogaloideae, Oziroëoideae and Urgineoideae (Speta 1998b, Pfosser & Speta 1999, Manning *et al.* 2004, Martínez-Azorín *et al.* 2011), a treatment that we favour here. Alternatively, Hyacinthaceae is treated as Asparagaceae subfamily Scilloideae, and consequently the former subfamilies are reduced to the tribes Hyacintheae, Ornithogaleae, Oziroëeae and Urgineeae (APG 2009, 2016, Chase *et al.* 2009).

In recent decades, the generic circumscriptions of subfamily Urgineoideae have been especially controversial (Martínez-Azorín *et al.* 2013a, 2013b, 2016, Crouch & Martínez-Azorín 2015). On the one hand, Manning *et al.* (2004) presented an extremely broad treatment, where only two genera were recognised for the whole subfamily: *Bowiea* Harvey ex Hooker (1867: t. 5619) and *Drimia* Jacquin (1797: 38), the latter including in synonymy several traditionally accepted genera which are easily identified by distinct syndromes of morphological characters, such as *Litanthus* Harvey (1844: 314), *Rhadamanthus* Salisbury (1866: 37), *Rhodocodon* Baker (1880: 280), *Schizobasis* Baker (1873: 105), *Tenicroa* Rafinesque (1837: 52), *Thuranthos* Wright (1916: 233), and *Urginea* Steinheil (1834: 321).

On the other hand, Speta (1998a, b, 2001) and Pfosser & Speta (2001) favoured a more analytic approach, in which about 20 different genera were accepted. However, several of these genera have proved to be para- or polyphyletic (Pfosser & Speta 2001, 2004, Manning *et al.* 2004, Pfosser *et al.* 2012). Speta (1998a) himself commented that 'the definition of genera in this subfamily is often unsatisfactory'. A similar scenario is found in the sister subfamily Ornithogaloideae, where contrasting taxonomic treatments were recently proposed based on different approaches (Speta 1998a, Manning *et al.* 2004, 2009, Martínez-Azorín *et al.* 2011). However, as shown by Martínez-Azorín *et al.* (2011), when sufficient plastid and nuclear DNA regions are included in the phylogenetic analyses, consistent morphological elements are fully congruent with clades, and these can be accepted at the generic rank. A similar study in Urgineoideae is ongoing that supports the recognition of a multigeneric treatment in the subfamily (M. Martínez-Azorín and collaborators, in preparation).

Accepted by Lorenzo Peruzzi: 30 Aug. 2017; published: 19 Sept. 2017

Van Jaarsveld & Van Wyk (2005) described two new species of *Drimia* –*D. cremnophila* Van Jaarsv. in Van Jaarsveld & Van Wyk (2005: 81) and *D. mzimvubuensis* Van Jaarsv. in Van Jaarsveld & Van Wyk (2005: 83)– from the eastern regions of the Eastern Cape Province of South Africa with similar flower morphology and a distinct androecium morphology. Martínez-Azorín *et al.* (2013b) described the genus *Sagittanthera* Martínez-Azorín *et al.* (2013b: 46) to include two species, *S. cyanelloides* (Baker 1897: 444) Martínez-Azorín *et al.* (2013b: 48), the generitype in which *D. cremnophila* is accepted as a synonym, and *S. mzimvubuensis* (Van Jaarsv. in Van Jaarsveld & Van Wyk 2005: 83) Martínez-Azorín *et al.* (2013b: 51).

Our recent studies on living material evidenced clear morphological and genetic differences among the two species of *Sagittanthera*. Therefore, following the same morphological and molecular criteria adopted in other subfamilies for generic circumscription (Martínez-Azorín *et al.* 2011) we here describe a new genus, *Aulostemon*, to include *S. mzimvubuensis*.

Materials and methods

Detailed morphological studies were undertaken on cultivated specimens following the terminology used for species of Hyacinthaceae in Martínez-Azorín *et al.* (2007, 2009). Seed sizes are expressed as L-H-W, meaning Length-Height-Width. Herbarium specimens from the herbaria ABH, B, BLFU, BM, BOL, E, G, GZU, GRA, HAL, K, L, LINN, M, MO, NBG, NU, NY, P, PRE, S, TCD, UPS, WU, Z, ZSS and ZT (acronyms according to Thiers 2017) were studied. Authors of the cited taxa follow IPNI (2017). Orthography of geographical names and grid-number system follows Leistner & Morris (1976).

Description of the new genus

Aulostemon **Mart.-Azorín, M.B.Crespo, M.Pinter & Wetschnig** *gen. nov.* (Fig. 1)

Similar to Sagittanthera, *but differing by the connation of the filaments of the stamens that are as long as or slightly longer than the anthers and form a distinct tube that surrounds the gynoecium (not much shorter than the anthers and free in the former); the free anthers (not connate at least along the distal half); the adaxial side of tepals exhibiting basal green maculae that connect to form a basal green ring (not completely white); and the absence of bracteoles.*

Typus generis:—*Aulostemon mzimvubuensis* (Van Jaarsv.) Mart.-Azorín, M.B.Crespo, M.Pinter & Wetschnig *comb. nov.* (holotype).

Basionym:—*Drimia mzimvubuensis* Van Jaarsv. in Van Jaarsveld & Van Wyk (2005: 83) ≡ *Sagittanthera mzimvubuensis* (Van Jaarsv.) Martínez-Azorín *et al.* (2013b: 51). Type:—SOUTH AFRICA. Eastern Cape Province. Port St. Johns (3129CB), lower Mzimvubu River, south facing shale cliffs near Lutengela, *Van Jaarsveld, Xaba, Harrower & Zwide 58* (PRE! holotype)

Bulbous geophyte. Bulb partially epigeal, with thickened, fleshy, semitranslucent, loose, rounded and club-shape scales, with short, flattened stalks, easily proliferating when detached, not producing threadlike structures when broken. Roots thickened and branched. Leaves 1–4 per bulb, linear, up to 50 cm long, 2–3 mm in diameter, leathery, dark green, subterete, slightly channelled on the adaxial side, finely striate with minute hairs. Inflorescence long racemose, the peduncle 25–40 cm long, the raceme long and lax, up to 20 cm long, with 20–50 nodding flowers, pedicels 14–20 mm long; the peduncle and pedicels long persistent and photosynthetic after seeds dispersal lasting from flowering time in spring to autumn. Bracts lanceolate, acute, 3–5 mm long, the lowermost with a long basal spur up to 8–9 mm long; bracteoles absent. Flowers pentacyclic, trimerous, stellate, nodding, opening in the afternoon. Tepals 6, biseriate, free from the base, outer tepals lanceolate, 10–11 × 2.5–2.8 mm, inner tepals oblong-lanceolate, 9–10 × 3–3.5 mm; adaxial side of tepals white with a green macula at the base that connect to form a green basal perigone ring; abaxial side of tepals white with a narrow central and longitudinal green band, the perigone also showing a green basal ring. Stamens 6, filaments flattened and connate along most of their length to form a distinct erect tube of ca. 3.5 mm long around the gynoecium, ending in short triangular lobes of ca. 1 mm long that bear free sagittate anthers of ca. 3 mm long and 0.8 mm wide at the base, dehiscing by minute apical pores and connivent to the style. Ovary ovoid, trigonous, ca. 2.8 × 1.8 mm, green. Style narrow, erect, ca. 4.5 mm long, straight, mostly included in the filaments tube and the connivent anthers, elongating to overtop the anthers after dehiscence of the latter. Stigma small and indistinctly trigonous. Capsule triloculate, loculicide, 7–10 × 5.4–7.5 mm, valves splitting to the base. Seeds numerous, flattened, suboblong, L-H-W 5.3–5.6 × 2.2–2.5 × 1.2–1.4 mm, black, with sinuous anticlinal testa cell walls (Figs. 1–2).

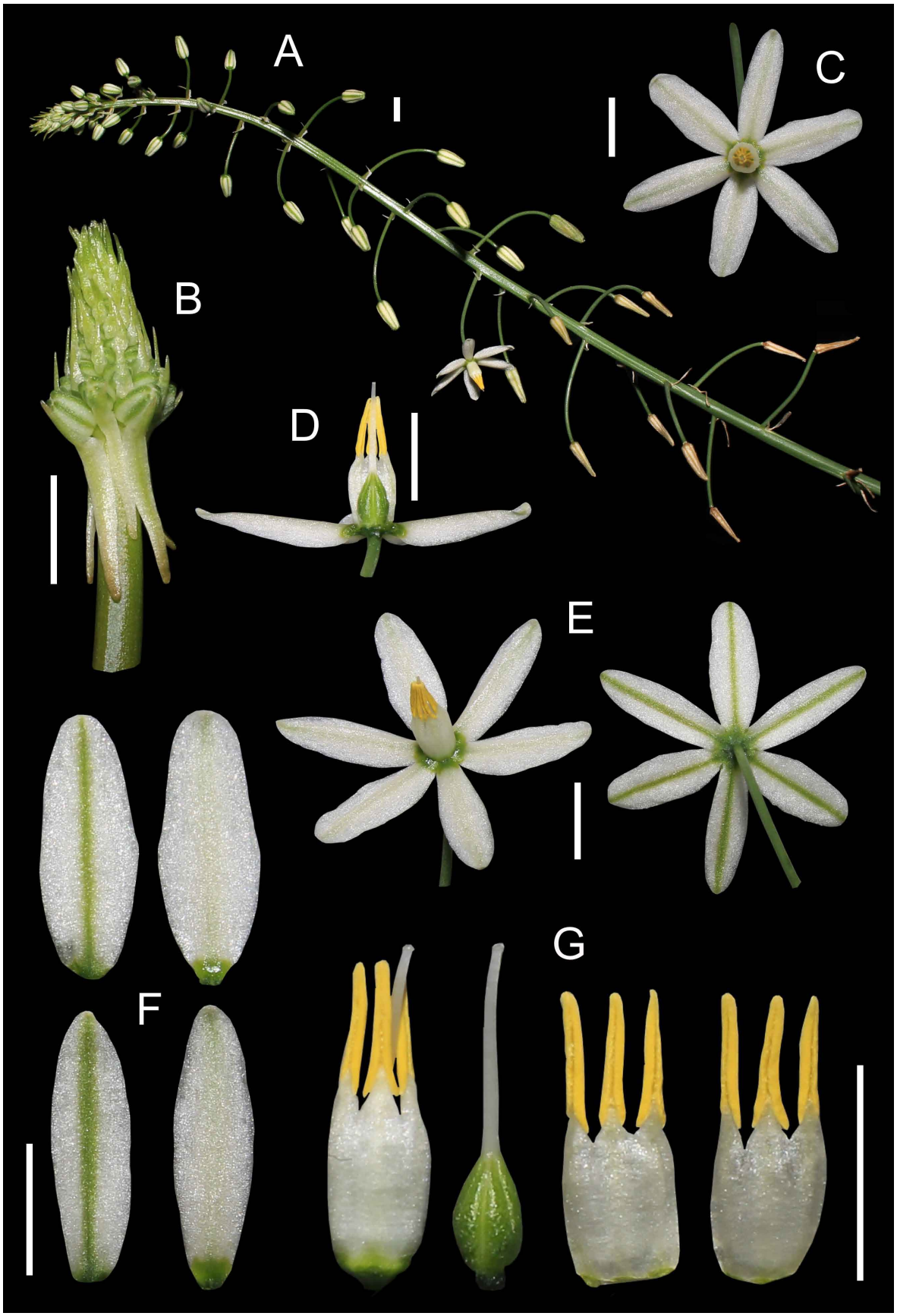

FIGURE 1. *Aulostemon mzimvubuensis* (Van Jaarsv.) Mart.-Azorín *et al.* in cultivation from the type locality, lower Mzimvubu River, near Lutengela, Eastern Cape Province of South Africa on 28 May 2014. **A.** Inflorescence; **B.** Young inflorescence showing bracts and long spurs; **C.** Flower, apical view; **D.** Flower with dissected androecium, lateral view; **E.** Flowers, adaxial (left) and abaxial (right) sides; **F.** Tepals, inners above and outers below, abaxial (left) and adaxial (right) sides; **G.** Androecium and gynoecium, dissected androecium on the right side, lateral views. Scale bars: 5 mm.

FIGURE 2. Seed of *Aulostemon mzimvubuensis* (Van Jaarsv.) Mart.-Azorín *et al.* in cultivation from the type locality, lower Mzimvubu River, near Lutengela, Eastern Cape Province of South Africa. Scale bar: 1 mm.

Etymology:—*Aulostemon* (*Aulos*, Greek name = tube, flute; -*stemon*, Greek = stamens). Named after its characteristic flowers, which show the filaments of stamens connate in a long tube.

Ecology and biogeography:—Rocky grasslands and crevices of vertical shale cliffs, usually south-facing, in thicket vegetation patches, associated with the Eastern Valley Bushveld and Bhisho Thornveld (Mucina & Rutherford 2006), in subtropical region characterised by summer rainfall and few rains in winter (total yearly precipitation ca. 500−1000 mm), and infrequent occurrence of frost.

Distribution:—Eastern parts of the Eastern Cape Province of South Africa, only known from NW of Port St. Johns along the Mzimvubu (uMzimvubu) River gorge.

Taxonomic and phylogenetic notes:—Martínez-Azorín *et al.* (2013b) described *Sagittanthera* to include *S. cyanelloides* and *S. mzimvubuensis* based on the unique syndrome of morphological characters and the general appearance of their flowers, especially regarding the androecium morphology that is linked to buzz pollination, and similar biogeography. At the time of the description of *Sagittanthera*, these authors studied living material in cultivation of *S. cyanelloides*, from which the buzz pollination experiments were performed, but no living material was available of *S. mzimvubuensis*. We were recently able to study living plants from the type locality of this latter species in cultivation (Fig. 1). This study evidences important morphological differences between the two species of *Sagittanthera* regarding characters that have been used in other subfamilies of Hyacinthaceae to segregate genera, such as connation of filaments and anthers, colour of tepals or presence of bracteoles (Table 1). *Sagittanthera* was described as having connate anthers (Martínez-Azorín *et al.* 2013b). However, the study of fresh material of *S. mzimvubuensis* revealed that the anthers in this latter species are free but connivent to the style (Fig. 1D, G), a character overlooked when studying photographs and herbarium material by Martínez-Azorín *et al.* (2013b). This renders the connation of the anthers along their distal half as a unique morphological character of *S. cyanelloides* in the whole family Hyacinthaceae, making recognition of *Sagittanthera* in a narrow sense very easy. Another interesting difference between the two *Sagittanthera* species is the presence of green basal maculae on the adaxial side of tepals in *S. mzimvubuensis* that form a green ring at the base of the perigone (Fig. 1). This is also present on the abaxial side of perigone in a lower degree, whilst the adaxial side of tepals in *S. cyanelloides* is white (sometimes the darker longitudinal dorsal band of tepals is somewhat visible). The presence of green basal maculae of tepals has been used to recognize the recently described genus *Mucinaea* M.Pinter, Mart.-Azorín, U.Müll.-Doblies, D.Müll.-Doblies, Pfosser & Wetschnig in Pinter *et al.* (2013: 296), that is easily distinguishable by its purplish-pink tepals bearing a double-eyed green floral marking at their base, surrounded by a white margin, unique within Hyacinthaceae (Pinter *et al.* 2013). The presence of green maculae in *S. mzimvubuensis* also supports its independence from *Sagittanthera* in a narrow sense, being also unique within subfamily Urgineoideae, although the green markings in *S. mzimvubuensis* are different from those in *Mucinaea*. The presence of bracteoles has also been described as a general character of *Sagittanthera* (Martínez-Azorín *et al.* 2013b). However, *S. mzimvubuensis* lacks bracteoles, therefore differing from the type species in a character used for generic circumscription in Hyacinthaceae (Speta 1998a, 1998b, 2001, Martínez-Azorín *et al.* 2011). Moreover, filaments of stamens in both species of *Sagittanthera* are very different. Whilst *S. cyanelloides* presents free filaments that are much shorter than the connate anthers, *S. mzimvubuensis* exhibits a long tube formed by the connation of the filaments that surrounds the gynoecium, supporting free but connivent anthers. Connation of filaments was the base to recognize genera in other subfamilies, such as *Neopatersonia* Schönland (1912: 251) (Martínez-Azorín *et al.* 2011). It is therefore remarkable, that *S. mzimvubuensis* is unique within subfamily Urgineoideae in having connate filaments allowing easy identification and supporting the description of a new monotypic genus. Other differences in vegetative characters

between the two species of *Sagittanthera* regard the formation of threads in the bulb scales of *S. cyanelloides* when broken (not produced in *S. mzimvubuensis*), the broad, flattened and distinctly keeled leaves of *S. cyanelloides* (narrower and subterete in *S. mzimvubuensis*), and the long persistent and photosynthetic stem and pedicels of the inflorescence after seeds release in *S. mzimvubuensis* (not soon withering after flowering in *S. cyanelloides*). These character states also evidence the morphological differences between both species. Our phylogenetic studies based on three plastid regions (ycf, matK and trnL-trnF) and a nuclear one (Agt1) include more than 300 samples of Urgineoideae covering its whole distribution and most of the recognized species (M. Martínez-Azorín and collaborators, in preparation). Our results (not shown) recover *S. cyanelloides* and *S. mzimvubuensis* in isolated positions within the subfamily and placed far from each other (M. Martínez-Azorín and collaborators, in preparation). Whilst *S. cyanelloides* is located as sister to *Thuranthos* and *Urginavia* Speta (1998b: 86), *S. mzimvubuensis* forms a different branch sister to *Rhadamanthopsis* (Obermeyer 1980: 137) Speta (1998b: 74). According to the data shown above, remarkable morphological and genetic differences existing between *S. cyanelloides* and *S. mzimvubuensis* support their segregation as two distinct genera, and therefore, the description of the new genus *Aulostemon* to accommodate the former *S. mzimvubuensis*. Inclusion of *Sagittanthera cyanelloides* in a single genus together with *Thuranthos* and *Urginavia* would be highly disruptive, as both latter genera show very different flower morphology and free anthers. On the other hand, although *Aulostemon* (*A. mzimvubuensis*) is sister to *Rhadamanthopsis* (Obermeyer 1980: 137) Speta (1998b: 74), the latter genus has campanulate nodding flowers with connate tepals, and free filaments (in part adnate to the perigone tube) and anthers, what does not allow inclusion of *A. mzimvubuensis*.

TABLE 1. Main differences between *Aulostemon* and *Sagittanthera*.

	Aulostemon	***Sagittanthera***
Bulb scales	semitranslucent, with no threadlike structures when broken	fibrous with dense slimy threadlike structures when broken
Leaves	subterete	flat with a broad abaxial keel
Bracteoles	absent	present
Inflorescence	long persistent and photosynthetic after seeds release	soon withering after flowering
Adaxial side tepals colour	white with a green macula at base forming a green basal ring	white
Filaments	connate in a long tube that surrounds the gynoecium, as long as or longer that the anthers	free, much shorter than the anthers
Anthers	free but connivent to the style	connate at least along the distal half

Acknowledgements

This work was partly supported by Fundación Ramón Areces (Spain), and H2020 Research and Innovation Staff Exchange Programme of the European Commission, project 645636: 'Insect-plant relationships: insights into biodiversity and new applications' (FlyHigh). Ernst van Jaarsveld is thanked for providing living material of *Aulostemon mzimvubuensis* from the type locality. Rhodes University provided working facilities from October 2009 and November 2011. We thank the curators of the herbaria, who provided access to the specimens examined. Two anonymous reviewers and Lorenzo Peruzzi made interesting comments on the manuscript.

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